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UNITED STATES DEPARTMENT OF AGRICULTURE
FOREST SERVICE

INTERMOUNTAIN FOREST & RANGE EXPERIMENT STATION
OGDEN, UTAH 84401

USDA Forest Service
Research Note INT-96

1969

MOUNTAIN PINE BEETLE EMERGENCE IN RELATION TO DEPTH OF LODGEPOLE PINE BARK

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ABSTRACT

Phloem thickness is one of the important factors affecting mountain pine beetle (Dendroctonus ponderosae *Hopkins) survival in lodgepole pine* (Pinus contorta *Dougl.). Emergence holes made by adults which completed larval development within the trees were counted on two 6- by 6-inch areas of bark on each tree killed by the mountain pine beetle on twenty 1/10-acre plots. Various tree, stand, and site factors were also measured. Emergence holes ranged from none in bark 0.06 inch thick to an average of 120 per square foot where the bark was 0.18 inch thick. Emergence holes were most closely correlated with bark depth, and varied with stand density and plot elevation. The greatest proportion of thick-barked trees was in the large diameter classes.*

Infestations of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) appear to depend on trees of large diameter. Cognizant of this, we posed the question, what difference that might contribute to successful population buildup of the mountain pine beetle exists between lodgepole pine trees (*Pinus contorta* Dougl.) of small and large sizes? Hopping and Beall (1948) and Gibson (1943) showed that greater proportions of large rather than small diameter lodgepole pine trees were killed by the mountain pine beetle. Bedard (1938), in studies of mountain pine beetles in western white pine (*P. monticola* Dougl.), found that trees 10 inches in diameter at breast height (d.b.h.) produced proportionally fewer beetles than trees of larger diameter. Reid (1963) studied factors that affect populations of the mountain pine beetle. He concluded that survival was most closely related to diameter of the host tree but stated that the reason for this was not apparent. Cole and Amman (1969) verified the relation between lodgepole pine of large diameter and the mountain pine beetle in the present Wyoming infestation.

Depth of phloem in small and large trees is the most obvious difference related directly to bark beetles. Phloem serves as food for larvae of the mountain pine beetle. Thus the following hypothesis was formed: the number of mountain pine beetles completing development within a given area of bark depends on depth of phloem. This study was designed to test this hypothesis.

METHODS

Tree, stand, and site measurements were obtained from a portion of a lodgepole pine forest that had been infested by the mountain pine beetle for several years. These measurements were subjected to a multiple correlation analysis to determine which explained the most variance in numbers of beetle emergence holes observed in the trees.

Tree, stand, and site measurements.--Twenty 1/10-acre plots were located in a grid pattern over a 2-mile-square portion of a lodgepole pine forest on the Teton National Forest where no effort had been made to control the mountain pine beetle. The year in which each tree was killed by the beetle was determined by using foliar characteristics (Cole and Amman 1969).

Variables measured on each tree were the numbers of holes made by emerging beetles that had completed development on two 6- by 6-inch areas of bark selected at random at d.b.h., the depth of bark in the center of each area (ridges and scales excluded), tree d.b.h., and tree height. In addition, the number of trees (4 inches d.b.h. and greater) per one-tenth acre (stand density) and the elevation of the plot were recorded.

Because all trees were dead, it was essential to know (1) if the numbers of emergence holes could be used as a reliable indicator of numbers of beetles completing development and emerging from a given area of bark, and (2) if total bark depth could be used as an indicator of phloem depth. Significant relations between numbers of emerging beetles and emergence holes were established in the field for caged lodgepole pine (Reid 1963) and in slabs in laboratory cages (correlation coefficient 0.85).[1]

Bark measurements of 30 trees ranging from 7 to 19 inches d.b.h. showed a significant relation ($r = 0.81$) between phloem depth and total bark depth. These findings indicate that emergence holes reliably indicate numbers of emerging beetles and that total bark depth of a dead tree is a good indicator of phloem depth at the time the tree was attacked and killed by the beetle. Shrinkage was assumed to be proportional at all phloem depths in the dead trees.

Analysis.--Numbers of emergence holes were expanded to a square-foot basis. Using the largest data group (year 1964), numbers of emergence holes (the dependent variable) were machine plotted two-dimensionally over independent variables and three-dimensionally over paired combinations of independent variables. The forms of relationships were then developed manually on these plottings.

The forms were described algebraically and then subjected to a full-screen, multiple regression analysis. In this analysis, the numbers of emergence holes were fitted by least squares as a function of all additive combinations of the independent variables. Explanatory strengths of the variables were assessed on the basis of fitting order and the multiple correlation coefficients. This process was repeated for each of 3 years--1963-65. Too few trees were killed within the study area before or after these years to provide enough data for a meaningful analysis.[2]

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[1]Unpublished data, author's files.

[2]The assistance of Chester E. Jensen, Statistician, Intermountain Forest and Range Experiment Station, Ogden, Utah, in the analysis of data and his algebraic descriptions of curves are acknowledged gratefully.

RESULTS AND DISCUSSION

Bark depth was consistently and by far the strongest independent variable each year, explaining from 23 to 62 percent of the variance in numbers of emergence holes per square foot of bark surface. Nominal gains in the multiple correlation coefficient (R^2) were contributed when stand density and plot elevation were incorporated into interaction models. Less consistent and smaller improvements in R^2 were noted for all other combinations of the independent variables.

Beetle emergence holes.--The average numbers of beetle emergence holes varied from none in bark 0.06 inch thick to 120 per square foot in bark 0.18 inch thick (table 1). Bark less than 0.10 inch thick had few emergence holes (0-12), bark 0.10 to 0.13 inch thick had moderate numbers of emergence holes (8-36), and bark 0.14 inch or greater in thickness contained large numbers of holes (34-120).

The number of emergence holes in bark of a given thickness became less with year (fig. 1). Two possible causes are intraspecific competition and natural enemies. Cole (1962) demonstrated experimentally the effect of competition among mountain pine beetle larvae. As the number of inches of egg gallery and, hence, the number of eggs per unit of bark increased, competition among the resulting larvae also increased. Consequently, survival of beetles in a given area of bark decreased. In 1963, the amount of egg gallery may have been about optimum for maximum beetle production; in the next 2 years it may have been so great that larval competition reduced beetle production.

Parasite and predator populations could also cause a decline in beetle emergence. They increase over the life of a mountain pine beetle infestation and should have exerted their greatest influence on the pine beetle population in 1965.

Table 1.--Average numbers of emergence holes made by mountain pine beetles per square foot of bark surface in lodgepole pine trees of different bark depth during 3 years

Bark depth (inch)	Year					
	1963		1964		1965	
	Observations	Emergence holes	Observations	Emergence holes	Observations	Emergence holes
0.06	--	--	2	0	--	--
.07	1	4	5	2	--	--
.08	--	--	8	3	2	2
.09	--	--	12	4	8	6
.10	6	33	25	14	6	8
.11	11	15	23	12	14	36
.12	11	26	23	26	11	31
.13	5	30	12	24	9	31
.14	2	80	4	61	3	43
.15	6	75	3	51	1	42
.16	2	34	2	50	1	84
.17	5	87	--	--	--	--
.18	2	120	4	83	2	36
.19	2	88	1	105	1	56

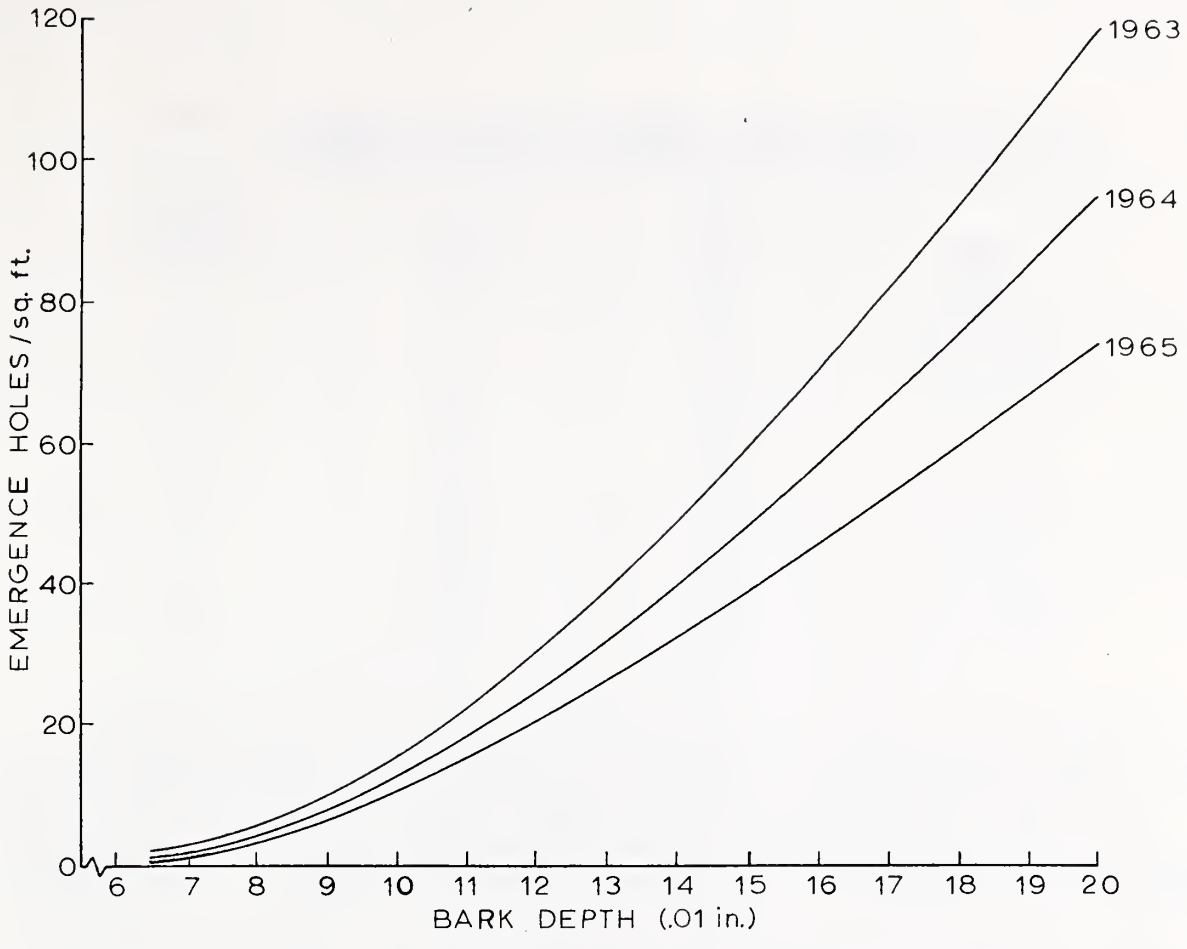

Figure 1.--The relation of mountain pine beetle emergence holes to bark depth of lodgepole pine killed.

(1963, $\hat{Y} = -9.6 + 4.111\ (100\ B\text{-}6)^{1.3}$, $R^2 = 0.44$;

1964, $\hat{Y} = -8.9 + 3.361\ (100\ B\text{-}6)^{1.3}$, $R^2 = 0.62$;

1965, $\hat{Y} = -3.0 + 2.494\ (100\ B\text{-}6)^{1.3}$, $R^2 = 0.23$).

Bark depth and d.b.h.--Bark depth was related to d.b.h. of the trees, the larger diameter trees generally having thick bark, and the smaller diameter trees usually having thin bark. Bark depth varied from an average of 0.082 inch on trees 7 inches d.b.h. to 0.161 inch on trees 18 inches d.b.h. or greater (table 2). Because phloem depth was correlated with total bark depth, the larger trees usually afforded more food for the mountain pine beetle per unit area of bark than smaller trees. However, the range in bark depth in each diameter was considerable (table 2) and it will be shown later that the relation of beetle emergence holes to d.b.h. is poor when compared to the relation to bark depth.

Factors affecting numbers of emergence holes.--In 1964 (year of peak tree mortality), bark depth explained 62 percent of the variation observed in numbers of emergence holes. Individual correlations with d.b.h., tree height, stand density, and plot elevation explained only 5 to 15 percent of the variation (table 3).

Table 2.--Average bark depth of lodgepole pine trees of different diameter killed by the mountain pine beetle

D.b.h. (inches)	Samples	Bark depth	Range
	No.	Inch	Inch
7	6	0.082	0.07-0.09
8	16	.097	.07- .13
9	33	.100	.06- .13
10	38	.101	.07- .15
11	40	.108	.08- .15
12	21	.118	.07- .15
13	32	.120	.09- .18
14	22	.126	.08- .16
15	10	.134	.12- .17
16	14	.137	.10- .19
17	12	.144	.10- .18
18+	14	.161	.11- .19

Combinations of three variables, with bark depth included in each combination, explained an additional 1 to 4 percent variation over that of bark depth alone (table 3). Combinations of four or more variables explained no additional variation. The significant independent variables appear to be bark depth, stand density, and plot elevation. These three variables explained all but 1 percent of the variation accounted for by all variables combined. The total variation explained in the numbers of emergence holes was 66 percent.

In 1963, bark depth was the most important factor measured, followed by stand density. Stand density contributed an additional 2 percent to the amount of variation explained in numbers of emergence holes over that of bark depth alone. The combination of bark depth, stand density, and elevation explained an additional 4 percent of the variation, giving a total of 48 percent, which was all but 1 percent explained by all variables combined.

Table 3.--Proportion of variance in numbers of mountain pine beetle emergence holes per square foot explained by different combinations of tree and stand factors

Variable		R^2		
		Year		
Dependent	Independent	1963	1964	1965
Emergence holes	Bark depth	0.44	0.62	0.23
	D.b.h.	.01	.06	.16
	Height	.02	.05	.02
	Stand density	.09	.15	.16
	Plot elevation	.03	.06	.14
	Bark depth X d.b.h.	.43	.63	.24
	Bark depth X height	.44	.64	.23
	Bark depth X stand density	.46	.64	.30
	Bark depth X plot elevation	.38	.66	.28
	Bark depth X stand density X elevation	.48	.65	.34
	All variables	.49	.66	.35

In 1965, stand density explained an additional 7 percent of the variation in numbers of emergence holes over bark depth alone. Again, the combination of bark depth, stand density, and elevation accounted for all but 1 percent of the variation (35 percent) explained by all variables.

In all years, the interaction between bark depth and stand density may be significant, contributing an increasing amount to R^2 over the 3 years (table 3). Trees growing in plots having the least stand density had the largest number of emergence holes for a given bark depth (fig. 2). The data do not demonstrate why this should be, but it is probably related to the ratio of phloem to dead bark. In dense stands, competition among trees may reduce the ratio.

A second interaction that may be significant is that of bark depth and plot elevation. Gibson (1943) showed that tree killing by the mountain pine beetle declined as elevation increased. I found the greatest numbers of emergence holes occurred in trees at the low elevation (7,200 to 7,400 feet). Trees at the two highest elevations (7,500 to 7,900 feet and 8,000 to 8,400 feet) had about equal numbers of emergence holes for a given bark depth (fig. 3). Although the reason for this difference is unknown, climatic factors (as they affect the insect) are probably responsible.

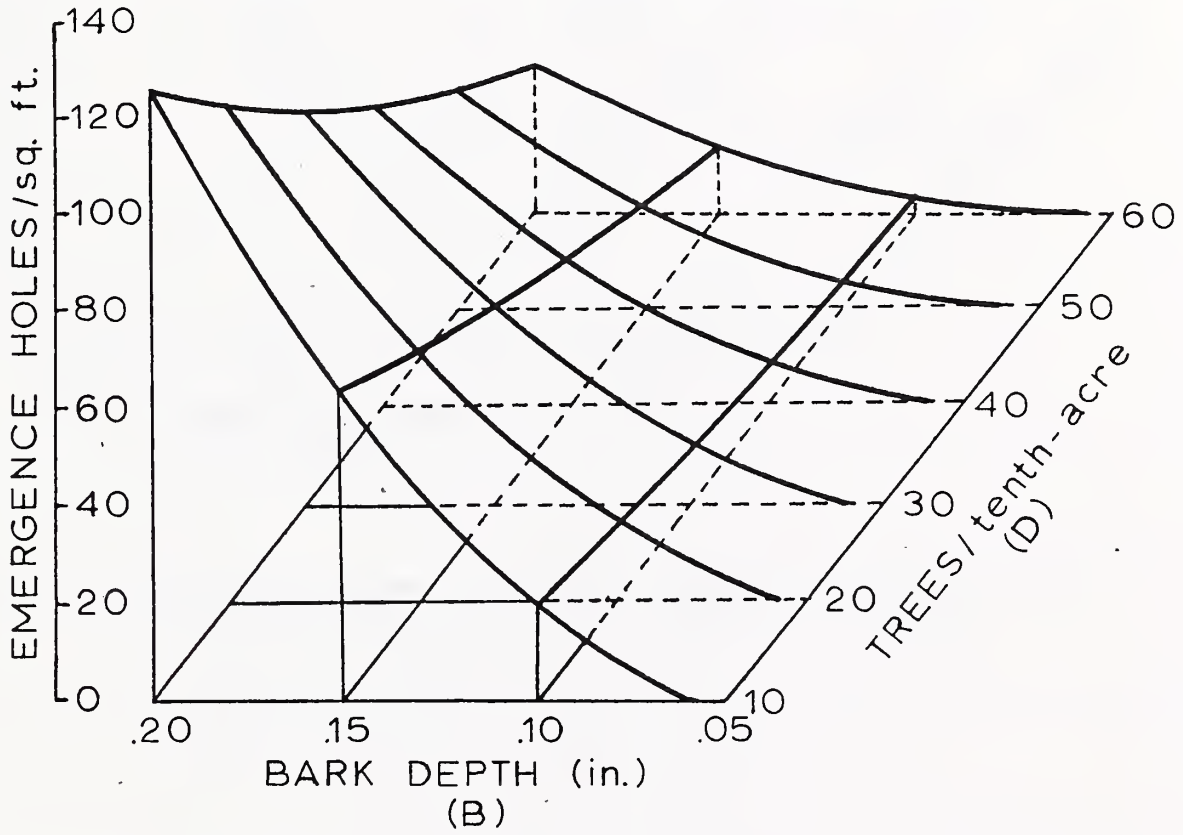

Figure 2.--The relation of mountain pine beetle emergence holes to bark depth of lodgepole pine killed in 1964 in stands of different density.

$$(\hat{Y} = -2.94 + 0.04046\ (100\ B\text{-}5)^{1.6}\ (10 - 0.1D)^{1.7}$$

$$0.06 \leq B \leq 0.20,\ 10 \leq D \leq 60;\ R^2 = 0.64).$$

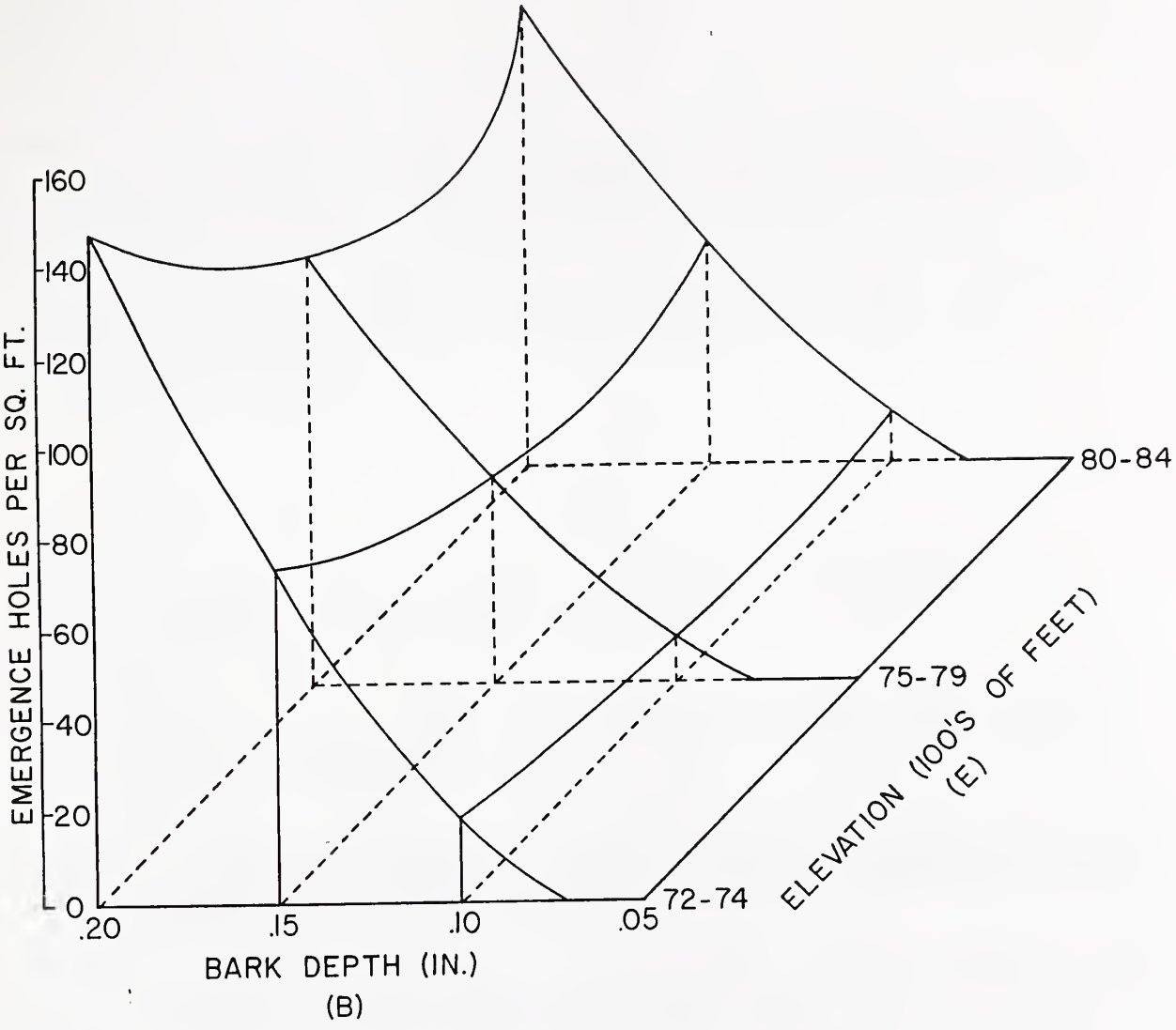

Figure 3.--The relation of mountain pine beetle emergence holes to bark depth of lodgepole pine killed in 1964 at different elevations.

$(\hat{Y} = -7.96 + 0.01571\ (100\ B-5)^{1.6}\ (E-77)^2 + 1.29\ (100\ B-5)^{1.6};$

$0.06 \leq B \leq 0.20,\ 72 \leq E \leq 84;\ R^2 = 0.66).$

CONCLUSIONS

Phloem depth (food) is probably the most important factor affecting epidemic populations of the mountain pine beetle in lodgepole pine. Although the relation of phloem depth to tree diameter is highly variable, most trees with thick phloem are large in diameter, while trees with thin phloem are usually small in diameter.

The exact role of phloem (quantity and quality) should be defined more precisely. In addition, other variables affecting beetle survival, such as intraspecific competition and natural enemies, need to be evaluated to improve predictions of mountain pine beetle populations.

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